

MULTILAMELLAR GROWTH IN TWO JURASSIC CYCLOSTOMATOUS BRYOZOA

by P. D. TAYLOR

ABSTRACT. The bryozoans *Reptomultisparsa incrustans* d'Orbigny and *Mesenteripora undulata* (Michelin) constructed multilamellar zoaria composed of a succession of overgrowing zoecial layers. The taxonomic status of the two species is reviewed briefly, and a mode of formation of the multilamellar zoarium common to both species is described. This involves overgrowth of old zoecia by young zoecia budded at C-shaped growth margins, the two ends of which remain stationary and function as points about which growth pivots. Complex patterns of growth result from the interactions between adjacent growth margins. The implications of this mode of growth to the colony during life are discussed.

As part of a current revision of the Jurassic cyclostomatous Bryozoa, the multilamellar species *Reptomultisparsa incrustans* d'Orbigny and *Mesenteripora undulata* (Michelin) have been re-examined. *M. undulata* occurs in the Bathonian and Callovian, where it encrusts a variety of substrates. *R. incrustans* attaches itself exclusively to the shells of Bathonian and ?Bajocian trochoform gastropods (Pl. 43, figs. 1, 2) and is known only from France. It is of special palaeoecological interest because most of the gastropod shells which it encrusted were occupied, subsequent to the death of the gastropod, by hermit crabs (Buge and Fischer 1970; Palmer and Hancock 1973). In addition, *R. incrustans* has a zoarial surface covered by monticules whose function was probably to provide a colonial water-current system for feeding purposes (Taylor, in press). The mode of growth of the multilamellar zoarium has not previously been described and the present study has shown how this is achieved in an identical manner in both species.

Material. *R. incrustans*. Bathonian of Ranville, Normandy: BMNH D2113, BMNH 60221, BMNH 60242.

M. undulata. Bathonian (Bradford Clay) of Bradford-on-Avon, Wiltshire: BMNH D2126, BMNH 35249, BMNH 35250. Bathonian (White Limestone) of Northleach, Gloucestershire: PDT 535, PDT 536. Bathonian of the Richmond boring, Surrey: BMNH D1911. Bathonian of Ranville, Normandy: BMNH D2088, BMNH 60346. 'Lower Oolite': BMNH B4850.

BMNH—British Museum (Natural History).

PDT—P. D. Taylor Collection, University of Durham.

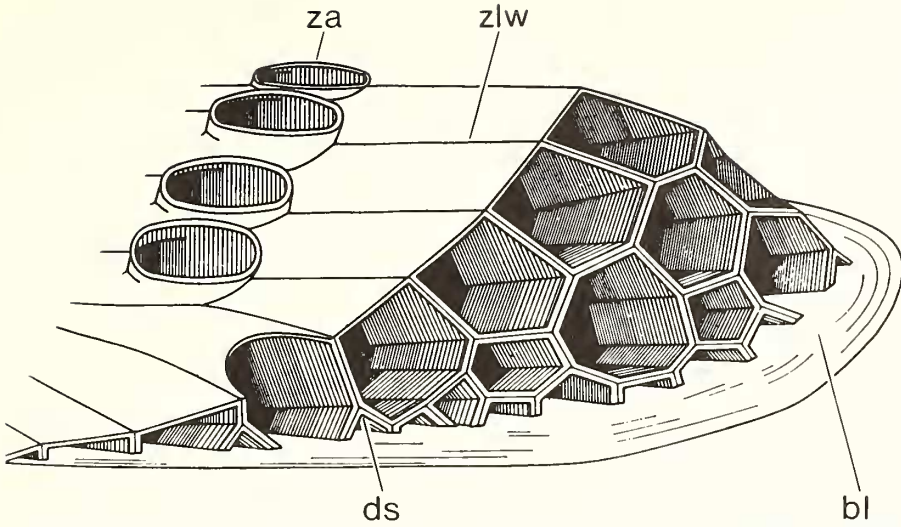
TAXONOMIC REMARKS

In 1852 d'Orbigny founded the genus *Reptomultisparsa* for multilamellar species allied to *Berenicea*. In it he included five species, two from the Jurassic and three from the Cretaceous. Two species of Bryozoa from the Jurassic were referred to the genus *Reptomultisparsa* by Gregory (1896). He considered the two Jurassic species described by d'Orbigny, *R. microstoma* and *R. diluviana*, to be synonymous and he gave

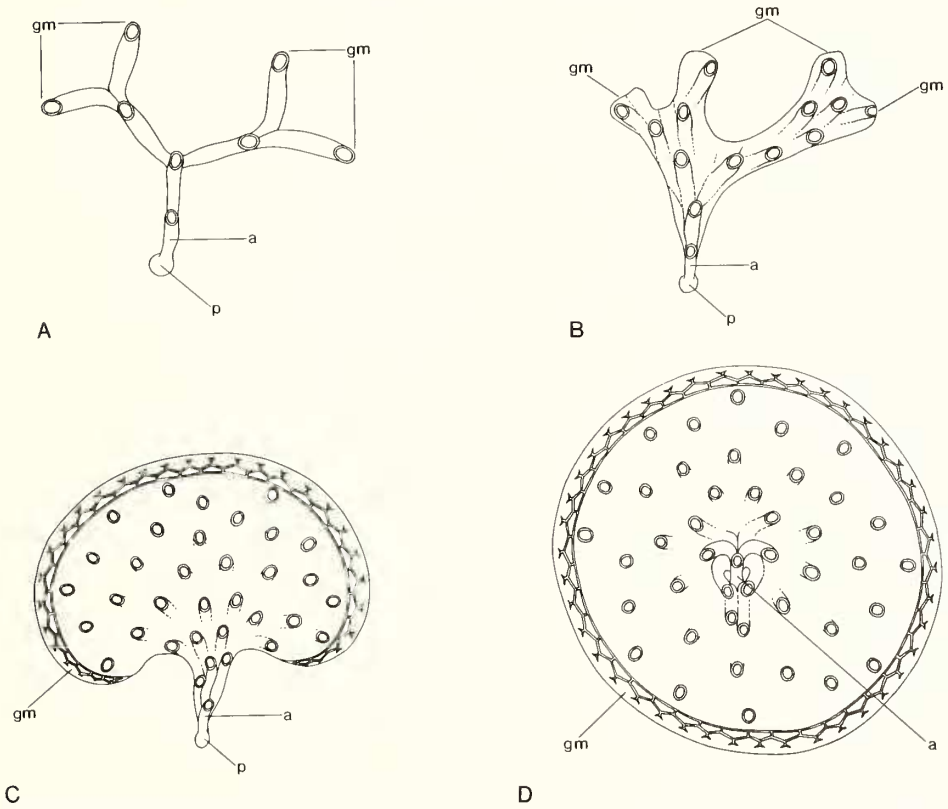
R. microstoma priority, designating it the genotype of *Reptomultisparsa*. In addition, Gregory also introduced a form, initially described by Michelin in 1846 under the name *Diastopora undulata*, into the genus *Reptomultisparsa* as *R. undulata* (Michelin). However, Gregory (1896, p. 113) himself cast doubts on the validity of the genus *Reptomultisparsa*, stating that 'the whole of the Tubuliporidae (genera included in the suborder Tubuliporina by Bassler 1953) ought to be formed into one genus. So long as it is recognised that the genera in this group are of no absolute value, but are only used as a matter of relative convenience, it is wisest to accept them, and *Reptomultisparsa* has as good a claim to recognition as the rest'. Taxonomic division of the Tubuliporina based on growth form is now known to be of limited value and it has generally been replaced by a method largely utilizing the form of the ovicells (Canu 1918). In 1969 the results of a restudy of Jurassic Bryozoa by Walter were published. His classification of the cyclostomes, relying heavily on the character of the ovicells, left *R. microstoma* in the redefined genus *Reptomultisparsa* (see Walter 1969, p. 75) but removed *R. undulata* from *Reptomultisparsa* into *Mesenteripora* (Walter 1969, p. 107). Walter (1969) considered that the form described by Gregory as *R. microstoma* is not the same as that described by d'Orbigny (1852) under the same name, but does agree with a form described by d'Orbigny in 1850 as *D. incrustans* and later in 1852 as *R. diluviana*. Thus Gregory's view that d'Orbigny's two Jurassic species of *Reptomultisparsa* are synonymous is incorrect. Both *D. incrustans* d'Orbigny and *R. diluviana* d'Orbigny were referred to *R. incrustans* d'Orbigny by Walter. *Atractosoezia*, with *A. edwardsi* as its genotype, was introduced by Canu and Bassler in 1922. Walter (1969) placed *R. incrustans* and *A. edwardsi* in synonymy. The view of Buge and Fischer (1970) that the synonymy cannot be accepted without a decision of the International Commission on Zoological Nomenclature seems incorrect, for this is a subjective and not an absolute synonymy. Brood (1972) considered that there is no significant difference in ovicell structure between *Reptomultisparsa*, *Mesenteripora*, and *Diastopora*. Therefore, on the grounds of priority, both *Reptomultisparsa* and *Mesenteripora* should be included in *Diastopora*. The validity of this view depends on a more extensive study of cyclostomatous Bryozoa and, for the present, the names *R. incrustans* and *M. undulata* are retained.

MODE OF GROWTH AND COLONY FORM IN ADNATE TUBULIPORINIDEAN BRYOZOA

In adnate tubuliporinidean Bryozoa, new zooecia are budded off by septal division on a basal lamina. A vertical septum separating two zooecia bifurcates at its junction with the basal lamina, the split widens and extends upwards as growth continues, and a new zooecium is thus partitioned off (text-fig. 1). This process occurs at the growth margin of the colony, which was shown by Borg (1926) to be enclosed beneath a common (hypostegal) coelom during life and which he termed the common bud. The longitudinal axis of each zooecium is oblique to the basal lamina for most of its length, but distally it bends upward to meet the zoarial surface at a high angle. The form taken by the adnate zoarium is controlled largely by its relative rate of lateral expansion, which in turn depends upon the frequency of zooecial budding. If there is no lateral expansion, then a uniserial branching zoarium of the stomatoporiiform type is developed (text-fig. 2A). A limited rate of lateral expansion produces



TEXT-FIG. 1. The growth margin of an adnate tubuliporinidean Bryozoa (after Illies 1968).
bl, basal lamina; ds, dividing septum; za, zoecial aperture; zlw, zoecial lateral wall.



TEXT-FIG. 2. Growth forms of adnate tubuliporinidean Bryozoa. A, stomatoporiform. B, probosciniiform. C, fan-shaped bereniciiform. D, discoidal bereniciiform. a, ancestrula; gm, growth margin; p, protoecium.

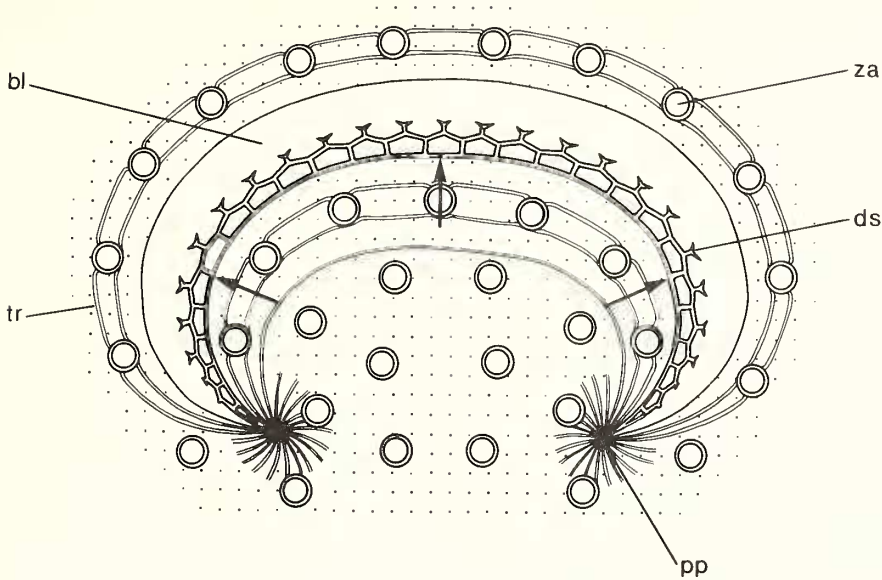
a zoarium of the multiserial probosciniiform type (text-fig. 2B), whereas a rapid rate of lateral expansion gives a multiserial bereniciiform type of zoarium. It may vary from fan-shaped (text-fig. 2C) to discoidal (text-fig. 2D). In the fan-like zoarium the growth margin is C-shaped, in the discoidal zoarium it forms a complete ring.

MODE OF MULTILAMELLAR GROWTH IN *REPTOMULTISPARSA*
INCRUSTANS AND *MESENTERIPORA UNDULATA*

Basic principles. All of the zoarial forms mentioned above consist of a single zooecial layer and are said to be unilamellar. In contrast, a multilamellar zoarium is formed by a sequence of bereniciiform zooecial layers (each floored by a basal lamina) occurring one on top of the other (Pl. 43, fig. 3), the oldest (i.e. astogenetically earliest) layer being at the base of the series, attached to the substratum. Multilamellar zoaria may arise in a variety of ways. Growth around a closed shape, from a single growth margin, can produce a multilamellar zoarium in which older zooecia would be covered by the subsequent extension of the growth margin which initially produced them. Alternatively, a multilamellar zoarium could be produced by a new zooecial layer being initiated proximally to the growth margin by the extrusion of secretory epithelium through a zooecial aperture on to the surface of the established zoarium. However, both of these modes of formation of multilamellar zoaria are excluded in *R. incrustans* and *M. undulata*, in which each zoarium possesses a number of discrete growth margins budding off zooecia in many different directions. Observations have shown that growth is continuous between zooecial layers, for it is not obvious where one layer ends and the next begins.

Patterns of growth of the multilamellar zoarium can be distinguished using zooecial lateral wall traces in *R. incrustans* (Pl. 43, fig. 8) and transverse calcareous ridges in *M. undulata*. In *R. incrustans* the traces of lateral bounding walls of zooecia can occasionally be discerned on the zoarial surface. They parallel the direction of growth of the zoarium and are therefore normal to the growth margin which secreted them. Thus the orientation of zoarial growth can be determined. The direction of zoarial growth is found from its orientation and from the fact that zooecial apertures are distally placed. Past positions of growth margins of *M. undulata* are indicated by closely spaced low calcareous ridges on the zoarial surface. These ridges are formed parallel to the growth margins and are transverse to the zooecia. Effectively, therefore, they are growth lines, their spacing reflecting the relative rate of growth.

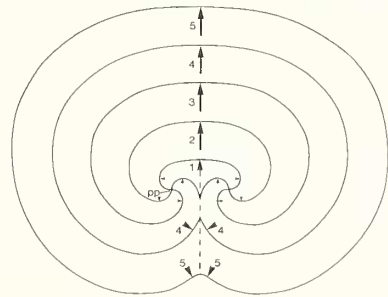
The transverse ridges are seen to converge at the ends of existing growth margins (Pl. 43, fig. 7). Therefore, growth must have been nil at these points, for they have remained stationary on the zoarial surface. Maximum separation between transverse ridges, and hence maximum growth rate, is located between the fixed ends of the growth margins. As a result, the two end points of a growth margin behaved as axes about which growth pivoted, and they may be termed pivot points. This mode of growth results in established zooecia being overgrown by newer ones orientated in exactly the same direction, as is seen in *R. incrustans* in which the lateral walls of young zooecia immediately proximal to a growth margin are parallel to those of the older zooecia they are overgrowing (Pl. 43, fig. 8). Near a pivot point, the zooecia



TEXT-FIG. 3. Simplified diagram of a C-shaped growth margin. Arrows indicate direction of growth. Zoarial surface stippled; bl, distal part of the basal lamina; ds, dividing septum in the region of zooecial budding; pp, pivot point; tr, transverse ridge; za, zooecial aperture.

are strongly and concentrically curved about that point. The typical features of the resultant C-shaped growth margin are shown in text-fig. 3.

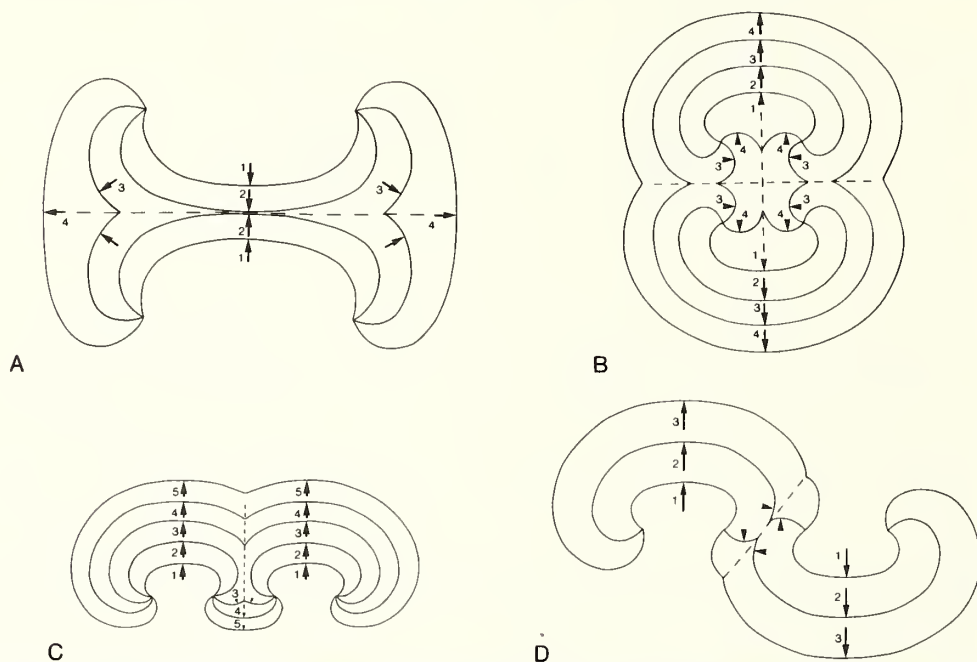
Growth at an isolated growth margin. Although interactions between adjacent growth margins are extremely frequent in these multilamellar Bryozoa, it is useful to consider the stages of growth of an isolated growth margin (text-fig. 4). The growth margin develops two lateral lobes which grow towards one another. Eventually the lobes meet and coalesce. Zooecia continue to be budded from each lobe, causing the line of anastomosis to lengthen in both directions. The anastomosis can be recognized by a band of irregularly, and closely, spaced apertures (Pl. 44, fig. 1). Anastomosis ceases when the zooecia being budded off by each lobe become parallel. A pair of growth margins at right angles to the line of anastomosis results. One of the growth margins is ring-like, lacks pivot points, and spreads outwards by budding off radially disposed zooecia. The other has the two original pivot points at its ends and soon



TEXT-FIG. 4. Growth at an isolated C-shaped growth margin arbitrarily divided into stages 1-5. Line of anastomosis dashed; pp, pivot point. Arrows indicate growth directions.

assumes a C-shaped form. It buds zoecia over those already formed to initiate a new cycle of growth. In this way each cycle of growth generates a ring growth margin and leaves behind a C-shaped growth margin (Pl. 43, fig. 6).

Interactions between adjacent growth margins. Before the lateral lobes of a growth margin have met, they invariably contact an adjacent growth margin. Some of the possible interactions between pairs of growth margins are illustrated diagrammatically in text-fig. 5. In cases A, C, and D, two C-shaped growth margins are left, whilst

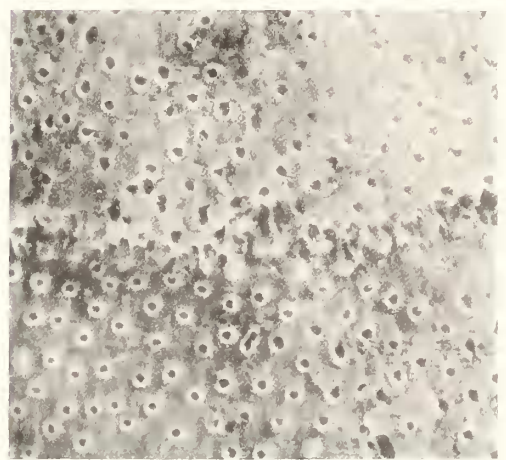
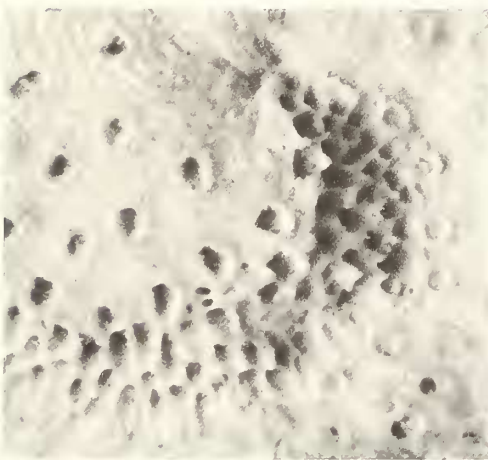
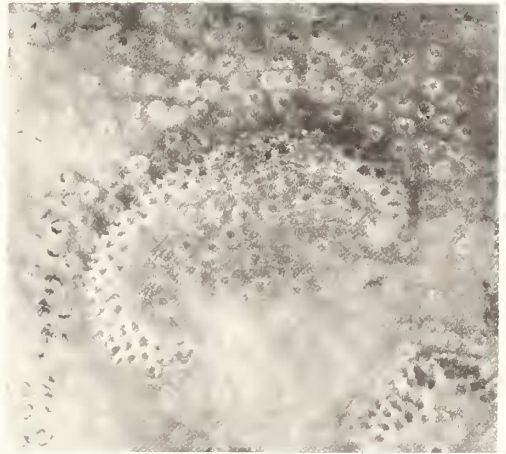
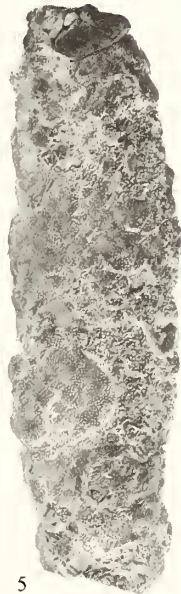
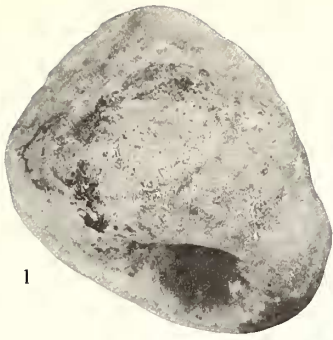


TEXT-FIG. 5. Interactions between pairs of C-shaped growth margins. A, growing towards one another. B, growing away from one another. C, adjacent and growing in the same direction. D, adjacent and growing in opposite directions. Lines of anastomosis dashed.

EXPLANATION OF PLATE 43

Figs. 1, 2, 8. *Reptomultisparsa incrustans* d'Orbigny. Bathonian, Ranville. 1, BMNH 60242, thick encrustation on a gastropod shell, $\times 2$. 2, BMNH 60221, acetate peel taken from a transverse section of a zoarium composed of about twenty zoecial layers encrusting a gastropod shell with sediment infilling, $\times 1.7$. 8, BMNH 60242, worn portion of a zoarium showing the zoecial lateral walls. The zoecia in the overgrowing layer are parallel to those which are being overgrown, $\times 14$.

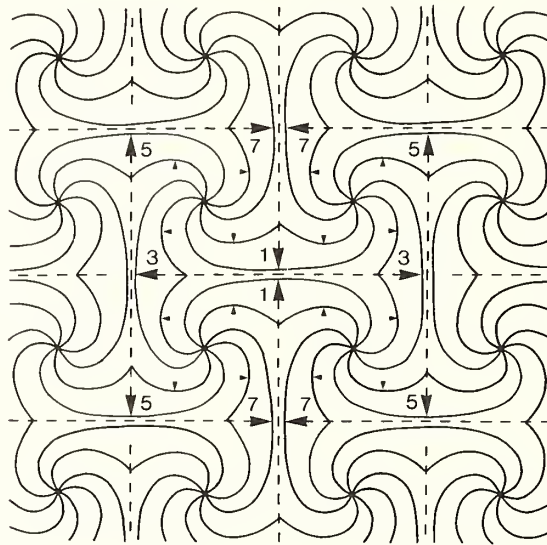
Figs. 3-7. *Mesenteripora undulata* (Michelin). Bathonian. 3, BMNH 35250, worn zoarium showing zoecial layers, Bradford-on-Avon, $\times 1.7$. 4, BMNH D2088, young zoarium encrusting an annelid tube, Ranville, $\times 1.9$. 5, BMNH B4850, zoarium intergrown with bereniciiform bryozoan on ?annelid tube, ?locality, $\times 1.1$. 6, BMNH B4850, characteristic C-shaped growth margin (the area figured by Gregory 1896, pl. VI, fig. 2), ?locality, $\times 14$. 7, BMNH D2088, transverse ridges converging on a pivot point at the end of a growth margin, Ranville, $\times 25$.



TAYLOR, growth in cyclostomatous Bryozoa

case B in addition generates a ring-like growth margin. The pivot points are retained in all cases, but resultant growth margins span pairs of pivot points different from those spanned by the original growth margins.

The four cases described for interaction between pairs of growth margins can be considered as end members from a series of possible interactions. Adjustment of the angle between the principal growth directions of adjacent margins allows further possible constructions. In addition, by altering the relative spacing between the pivot points, modification of the resultant growth pattern occurs. Further complexities arise when more than two growth margins are operative. If they are irregularly and/or closely spaced, then the interactions between them may produce very involved patterns of growth. Indeed, in practice, the spacing of pivot points determining the disposition of the growth margins is usually extremely irregular. However, to illustrate interaction between multiple growth margins, a theoretical arrangement is considered in which the pivot points are equally spaced in a rectilinear manner. The consequent pattern of zoarial growth is illustrated in text-fig. 6. Two growth margins meet,



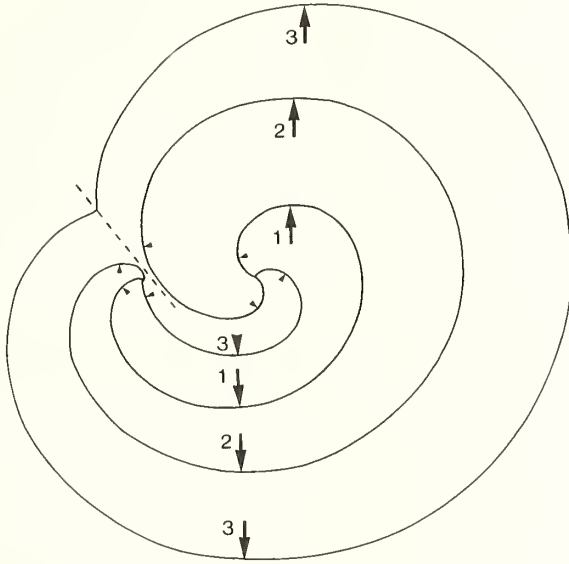
TEXT-FIG. 6. Growth pattern resulting from a rectilinear arrangement of pivot points. Cycle arbitrarily divided into eight stages, alternate stages numbered. Lines of anastomosis dashed.

anastomose, and produce a pair of growth margins growing at right angles to the original margins and in opposite directions to each other. They both subsequently anastomose with margins growing towards them and produce new margins normal to them. When four sets of growth margins, each normal to the preceding one, have been generated the cycle has returned to its starting point. An even covering of zoecia results.

The typical zoarium has a much more irregular disposition of its pivot points, frequently with an inner area of small irregularly arranged C-shaped growth margins.

By their coalescence these produce a surrounding area of larger, outward-spreading growth margins.

Modifications to the basic pattern of growth. Occasionally, the growth rates along the length of a C-shaped growth margin are asymmetrical, one side of the margin having a more rapid rate of growth than the other. When this occurs, the growth margin acquires a spiral appearance, often with a slight hummock at the apex of the spiral, where the growth rate is greatest. Growth margins of this type frequently develop in isolation, for the rapid growth rate at one side allows it to anastomose with the more slowly growing side (text-fig. 7), producing a ring-like growth margin which



TEXT-FIG. 7. Growth at an asymmetrical growth margin.
Line of anastomosis dashed.

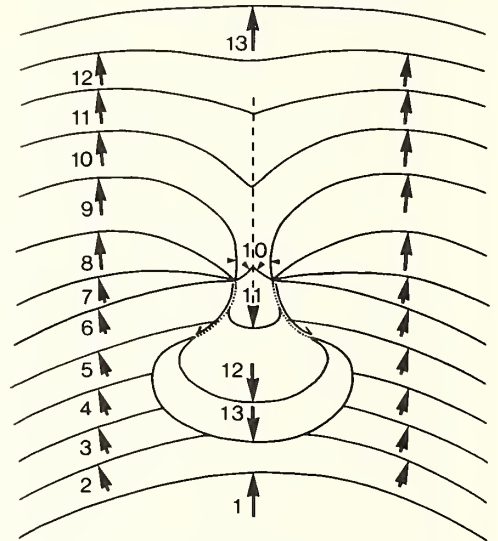
prevents the C-shaped growth margin from contacting other growth margins. One thick zoarium of *R. incrustans* (BMNH 60221) has apparently been formed wholly by an asymmetrical C-shaped growth margin, which has generated a succession of ring-like growth margins progressing from the apex towards the aperture of the encrusted gastropod shell.

Sometimes three or more growth margins converge at a point on the zoarium. They usually anastomose and growth ceases (Pl. 44, fig. 3). However, zoaria of *M. undulata* occasionally develop an erect habit, which almost certainly results from such a junction between three or more growth margins. The transition between encrusting and erect states has not been observed, but it seems probable that the basal laminae of converging growth margins on the adnate portion of the zoarium join to form a vertical axial lamina from which zooecia are budded to produce a cylindrical stem. If the axial lamina has been formed by the convergence of three growth margins, then in transverse section it will be Y-shaped, if by four growth margins, then it will be X-shaped,

etc. (see Walter 1969, pl. 11, fig. 4). New zoecial layers produced on the adnate portion of the zoarium may subsequently grow up the erect stem.

Pivot points are not always stationary on the surface of the zoarium. Sometimes a small rate of growth at a pivot point causes it to move slightly. The path of its migration is marked by a zoarial lateral wall which forms a discontinuity between the overgrowing and overgrown zoecial layers. Pivot-point migration is an important process during the formation of a stable pattern of pivot points in immature zoaria.

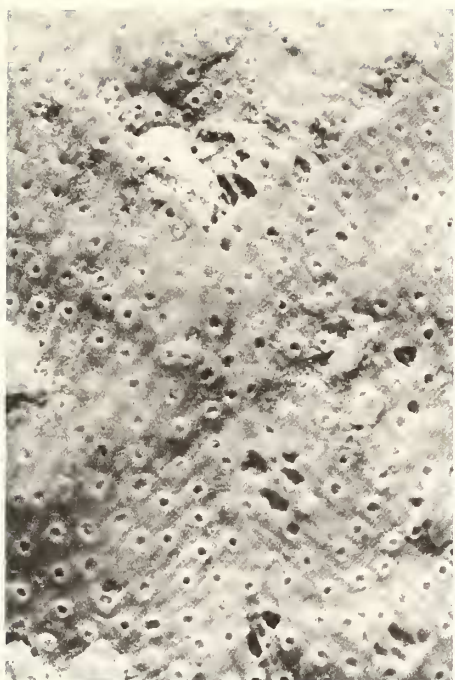
Young zoaria and the establishment of new pivot points. Although no very young zoaria have been examined, it seems likely that they are of the fan-shaped bereniciiform type (text-fig. 2c). The sides of the zoarium would be formed by zoarial lateral walls, the junctions of which with the growth margin can be looked upon as migrating pivot points. Eventually growth ceases at these points, and they become the first true pair of pivot points on the zoarium. Growth can now proceed in a manner similar to that described for the theoretical case of an isolated growth margin. Although this manner of growth will produce a series of ring-like growth margins, it is incapable of generating new pivot points and hence additional C-shaped growth margins. A mechanism for the formation of new pivot points must be sought, since mature zoaria usually possess a large number of C-shaped growth margins. A multilamellar zoarium could be adequately produced by a solitary C-shaped growth margin spanning a pair of pivot points, but the acquisition of additional pivot points would, however, allow a faster rate of overgrowth. The formation of new pivot points is displayed by an immature specimen of *M. undulata* (BMNH D2088) from the Bathonian of Ranville (Pl. 43, fig. 4). Growth ceases along a short length of the growth margin, thus establishing pivot points at the two ends of that length (text-fig. 8). What was



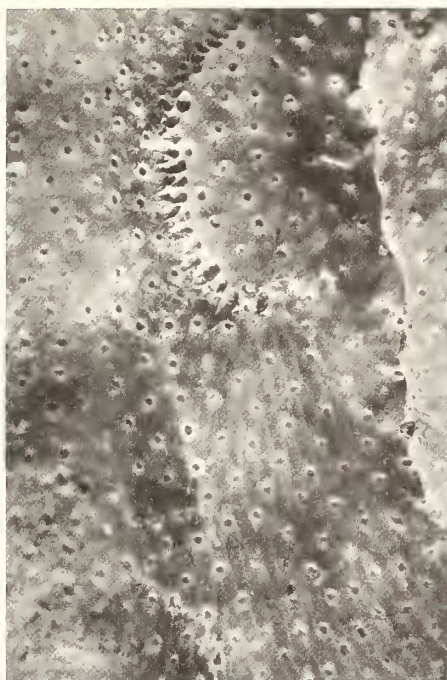
TEXT-FIG. 8. Formation of a new C-shaped growth margin. Line of anastomosis dashed. Zoarial lateral walls formed by pivot-point migration are dotted and marked with half arrows.

EXPLANATION OF PLATE 44

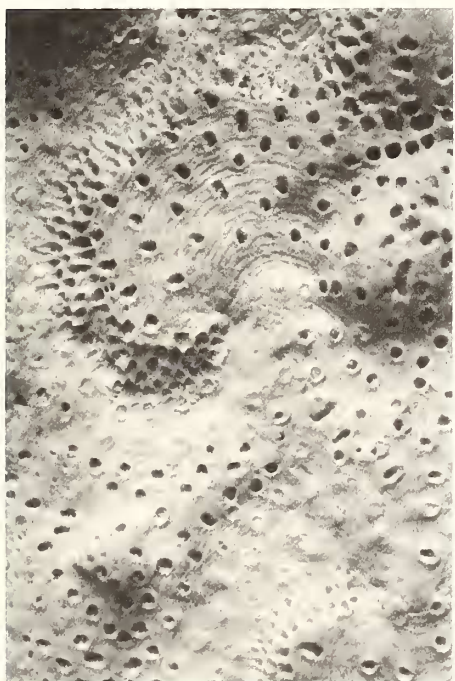
- Figs. 1, 2. *Reptomultisparsa incrustans* d'Orbigny. Bathonian, Ranville. 1, BMNH 60242, a line of anastomosis formed at the junction between growth margins budding off zoecia from the bottom left and bottom right, $\times 14$. 2, BMNH D2113, growth margin budding off zoecia parallel to those they are overgrowing, $\times 14$.
- Figs. 3, 4. *Mesenteripora undulata* (Michelin). Bathonian, Ranville. 3, BMNH D2088, growth margin terminated by a pivot point, left central. The elevated area at bottom left has been formed where three growth margins have converged, $\times 14$. 4, BMNH D2088, an unusual case in which a new growth margin, centre right, has been formed and has immediately divided. Both margins so formed would have eventually coalesced with the larger margin growing towards them, $\times 14$.



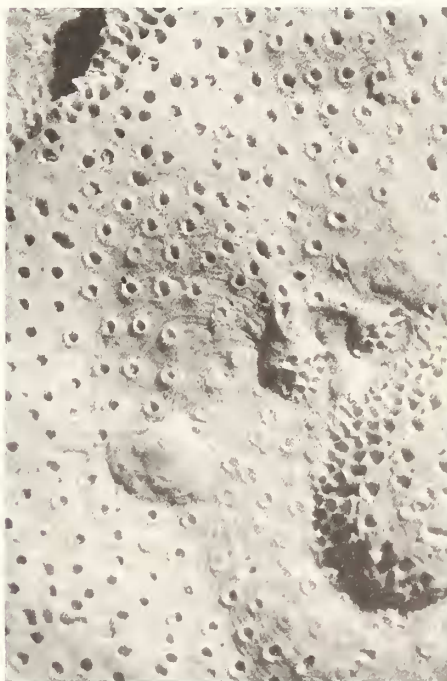
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TAYLOR, growth in cyclostomatous Bryozoa

originally a single growth margin has now become two growth margins, separated by the length at which growth has ceased. Each extends between one of the original pair of pivot points and one of the new pair. The two growth margins begin to extend lobes towards each other, in the manner of those shown in text-fig. 5C. The lobes anastomose, producing a large growth margin growing distally and a smaller one growing proximally. The pivot points of the small growth margin move apart whilst migrating proximally, their path being marked by zoarial lateral walls. When the pivot points are a sufficient distance apart (usually about 5 mm), growth ceases at them, and a conventional C-shaped growth margin results.

DISCUSSION

R. incrustans and *M. undulata*, belonging to the suborder Tupuliporina (Acamptostega of Borg 1926), are grouped with the single-walled stenolaematous Bryozoa of Borg (1926). In single-walled stenolaemates, a hypostegal coelom exists only over the growth margin, a region termed the common bud by Borg (1926). Where a common coelom exists, a relatively high degree of colonial co-ordination of growth is expected (Boardman and Cheetham 1973). Proximal to the growth margin, calcification takes place at the level of the individual; it is usually limited to the extension of zooecial tubes in the form of peristomes, and to the secretion of diaphragms. Zoarial growth in these single-walled forms is largely co-ordinated and determined by events occurring at the growth margin. Hence, the multilamellar growth of the species under consideration is predominantly controlled at the common buds or growth margins. Individual growth margins are not connected by a common coelom and therefore function fairly autonomously. However, co-ordination of calcification within them must be relatively precise to produce the observed variation of growth rates along their length. It is thought unlikely that growth at an encroaching growth margin is in any way guided or influenced by the disposition of the transverse ridges or zooecia in the layer being overgrown. Thus, the parallel nature of transverse ridges and zooecia in successive layers is simply a result of the intrinsic properties of the growth margins.

Where separate growth margins meet, continuity of soft tissues is achieved, and parts of these apparently separate later with onward extension of the growing edges. For example, in text-fig. 5A, a part of the common coelom covering each of the original two growth margins contributes to the common coeloms of the two resultant growth margins. The coalescence and unification of growth margins from different parts of a single colony after they have grown apart has been termed autosyndromy by Knight-Jones and Moyse (1961). It has been observed in a variety of Bryozoa (Stebbing 1973) and clearly occurs in these multilamellar species. Homosyndromy is the process of coalescence and unification of growth margins from separate colonies of the same species. Although less common than autosyndromy, homosyndromy is known to occur occasionally in Bryozoa. This raises the possibility that some specimens of *R. incrustans* and *M. undulata* may have a multiple origin.

The feeding water-current system of each polypide in a bryozoan colony draws water in at the top of the tentacle crown and passes it out at the sides between the tentacles (Borg 1926, fig. 10). Hence, exhalant water is directed towards adjacent polypides, a situation not desirable for the efficient feeding of the colony as a whole.

In many adnate tubuliporinideans, polypides are only found in the zooecia in a band a few millimetres wide just proximal to the growth margin (Silén and Harmelin 1974). This situation allows for the maintenance of an efficient colonial water-current system by permitting the exhalent water currents of the polypides to escape distally and proximally at the sides of this band. A similar arrangement probably occurred in colonies of *M. undulata* during life, for zooecia more than a few millimetres behind the growth margins are usually closed by terminal diaphragms and therefore cannot have protruded a polypide. Those zooecia adjacent to the growth margin are commonly open. Thus, the overgrowing zooecia of *M. undulata* always covered zooecia lacking polypides.

Banta *et al.* (1974) have suggested an alternative method by which an efficient colonial water-current system may have been maintained. This involves protuberances on the zoarial surface, known as monticules, which acted as areas for the collection and upward discharge of zooidal exhalant currents. Monticules have been described from *R. incrustans* (Taylor 1975). In this species it is suggested that functional polypides were present throughout the whole of the zoarium but were in a somewhat smaller concentration on the monticules, i.e. polypides were present well proximal to the growth margins. Sections through zoaria of *R. incrustans* show that many of the overgrown zooecial apertures were open and therefore could have protruded a polypide at the time of overgrowth. Hence, in colonies of *R. incrustans*, when the individuals reached a certain age (equivalent to the length of time it took for one cycle of overgrowth to be completed) they were probably smothered by an overgrowing zooecial layer. The covering of gerontic zooids seems less of a disadvantage when looked at in the light of polypide degeneration and brown body formation (Ryland 1970).

Multilamellar growth by the mechanism described allows all zooids an equal length of time before they are covered, and produces a zoarium of even thickness. Its prime advantage is that it enables a single colony to make the best possible use of a substratum by repeated encrustation, allowing a considerable increase in the life-span of a colony. In particular, where the number and extent of substrata are limited, a multilamellar zoarium has a special advantage. Hence, *R. incrustans* probably attached itself to the only substratum available at the time, namely shells inhabited by hermit crabs. It became highly adapted to its mode of life, by the acquisition of monticules and a multilamellar growth form. Attachment to the shell occupied by a hermit crab may have prevented the colony being covered by sediment accumulating at a relatively rapid rate. In contrast, adnate multilamellar zoaria of *M. undulata* could probably only have developed where there was a low rate of sedimentation.

The same mechanism for multilamellar growth has evidently arisen independently in two species which are taxonomically fairly well separated. Perhaps the potential for multilamellar growth by this method is present in other normally unilamellar adnate tubuliporinidean Bryozoa. It is hoped that a clearer understanding of the way in which adnate tubuliporinidean zoaria are constructed will be gained by application to other species of the principles of pivot point and anastomosis.

Acknowledgements. This work was carried out during the tenure of a N.E.R.C. research studentship, which I gratefully acknowledge. I wish to thank Dr. G. Larwood for supervision, and Miss P. L. Cook of the British Museum (Natural History) for criticizing the draft manuscript.

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Typescript received 15 July 1975